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STABLE CARBON ISOTOPE RATIOS OF THE PLANKTONIC FOOD WEB IN THE NORTHERN GULF OF MEXICO

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ABSTRACT

Analyses of stable carbon isotope ratios were conducted on components of the planktonic food web in the northern Gulf of Mexico to evaluate the importance of terrestrial organic matter as a source of carbon to this food web. These analyses were made on samples collected in areas of high (Southwest Pass, Louisiana) and low (Cape San Blas, Florida) riverine input. Dissolved organic carbon at 7 and 26 km from Southwest Pass and the 0.45–20 μm particulate organic carbon size fraction at 7, 26, and 43 km from the Pass were the only components that displayed isotope ratios approaching terrestrial carbon values, means of −24.0‰ and −24.6‰ respectively. Phytoplankton had a mean $\delta^{13}C$ of −22.7‰ for both northern Gulf areas, whereas three copepod genera and total zooplankton had mean values of −20.5‰ and −21.9‰, respectively. Four species of larval fish had similar $\delta^{13}C$ values in both areas (−21.1‰), suggesting their tissue carbon was derived ultimately from phytoplankton. Gut analyses indicated an intermediate zooplankton link for three species. Gulf menhaden appeared to derive their carbon directly from phytoplankton as well as through the phytoplankton-zooplankton pathway. Isotopic fractionation values between trophic levels did not exceed ±1.8‰, a range similar to that reported for other ecological systems.

The analysis of stable carbon isotopes has been employed extensively in geochemical studies to evaluate the source of organic carbon inputs to sediments (Craig, 1953; Sackett and Thompson, 1963; Parker, 1964; Parker et al., 1972; Shultz and Calder, 1976; Fry et al., 1977; Gearing et al., 1977). Marine organic carbon has an isotope ratio generally more positive than terrestrial organic carbon. In general, studies have shown more positive isotopic ratios in the sediments at increasing distances from shore. This observed gradient indicates an increasingly greater contribution of marine carbon to sediments in the seaward direction.

This type of analysis has been recently used to trace flows of carbon from plants to animals in aquatic food webs. Tracer studies of food webs are possible because the two stable isotopes of carbon, ^{13}C and ^{12}C, react at slightly different rates in photosynthetic reactions and because there is a dichotomy in the biochemistry of photosynthetic carbon fixation; terrestrial vascular plants have lower $^{13}C/^{12}C$ ratios or more negative $\delta^{13}C$ values than marine planktonic algae (Bender, 1971; Smith and Epstein, 1971). Marine phytoplankton collected in coastal waters of the southeastern Atlantic and Gulf of Mexico generally display $\delta^{13}C$ values of −18 to −22‰ (Haines, 1976; Fry et al., 1977; Fry and Parker, 1979); high latitude phytoplankton can display isotope ratios as negative as −26‰ (Gearing et al., 1977). Terrigenous sources found in rivers and estuaries normally are more negative (−24 to −34‰) (Shultz and Calder, 1976; Gearing et al., 1977). Individual plant species or groups possess unique stable carbon isotope ratios, and once organic matter acquires a specific ratio, it tends to retain that signature in a series of trophic level transfers (Tregunna et al., 1970; Bender, 1971; Smith and Epstein, 1971; Fry and Parker, 1979; McConnaughey and McRoy, 1979). Thus, the $\delta^{13}C$ value of a plant is primarily determined by isotope-kinetic effects in the photosynthetic fixation of carbon dioxide, while that of an animal is determined mainly by diet.

Carbon inputs from multiple sources and isotopic fractionation among trophic levels alter isotope ratios and can limit the precision of the technique (Deuser et

al., 1968; Fry and Parker, 1979; McConnaughey and McRoy, 1979), but in conjunction with food analyses, the technique is useful in identifying carbon transfer pathways. For example, bacterial species grown on glucose ($\delta^{13}C = -10.7‰$) have a value of about $-10‰$, while the same species grown on palmitic acid ($-22.4‰$) display a value of $-20.5‰$ (Jacobson et al., 1970). Zooplankton tend to display the same isotope ratio as phytoplankton (Land et al., 1975). Studies in shallow bays (Fry, 1977), salt marshes (Haines, 1976; 1977; Kneib et al., 1980), seagrass beds (Thayer et al., 1978; Fry and Parker, 1979; McConnaughey and McRoy, 1979), coral reefs (Black and Bender, 1976), and laboratory microcosms (Parker and Calder, 1970; DeNiro and Epstein, 1978) all show that animal $\delta^{13}C$ values either fall within the range of values for plants in their community or for animals that are food sources. As pointed out by DeNiro and Epstein (1978), the technique is best applied in situations where the diet is derived from sources with large differences in $\delta^{13}C$ values, such as terrestrial and aquatic plants.

The importance of terrigenous organic carbon as an energy source for coastal marine food webs, especially near river mouths, is poorly understood. The objective of our study was to identify carbon sources and to evaluate carbon linkages of planktonic food webs in the vicinity of Southwest Pass, Louisiana and Cape San Blas, Florida. We hypothesized that if terrigenous fixed carbon, either in particulate or dissolved form, were an important carbon source, components of the planktonic food web in the vicinity of the Mississippi River plume off Southwest Pass would display $\delta^{13}C$ values approaching terrestrial carbon signatures. The Cape San Blas area, however, does not normally receive the freshwater input as does the Delta area, and we hypothesized that particulate organics, zooplankton, and larval fishes would display a more marine carbon isotope signature in this region.

Area and Methods

Samples collected for stable carbon isotope analyses included dissolved organic carbon (DOC), size fractions of particulate organic carbon (POC), zooplankton, fish eggs, and larval fishes: gulf menhaden, *Brevoortia patronus*; spot, *Leiostomus xanthurus*; Atlantic croaker, *Micropogonias undulatus*; and white mullet, *Mugil curema*. Material from each of these components, however, was not collected from each sampling date and location (Table 1). Samples were collected at each of three stations on the 18, 91 and 183 m isobaths along two transects in the northern Gulf of Mexico (Fig. 1). Transect A was located off Southwest Pass, Louisiana, near or in the Mississippi River plume; the three stations were located approximately 7, 26, and 43 km from the entrance of the Southwest Pass, and surface salinity averaged 23, 29 and 36‰ respectively at each station for the three cruises. Transect B was located southwest of Cape San Blas, in an area not normally receiving large freshwater input; the three stations were 35, 61, and 78 km from Cape San Blas, and during the three cruises surface salinity averaged 36‰ at each station. Sampling was carried out in December 1979, February 1980, and December 1980 aboard the FRS Oregon II.

Water samples for DOC and POC were collected with 5-l Niskin water bottles at 1200 and 2400 h. In December 1979 and February 1980, samples were taken at surface, midwater and near bottom depths at each station. Water samples were pooled and filtered through a 125-μm followed by a 20-μm Nitex screen. Material retained on this 20-μm screen was backwashed onto a 0.45-μm Millipore AG45-025 silver filter and frozen. Subsequently from 1 to 5 l of the 20-μm filtrate were filtered through 0.45-μm filters and frozen; the 0.45-μm filtrate was taken as dissolved organic carbon following Jeffrey and Hood (1958). In December 1980, water depths sampled were as follows: A1—surface, 9, 11, 13 and 15 m; A2—surface, 25, 40, 75 and 85 m; A3—surface, 32, 66, 80 and 150 m; B1—surface, 3, 6, 9 and 12 m; B2—surface, 18, 35, 75 and 90 m; B3—surface, 50, 75, 100 and 150 m. Water samples were pooled from each station and filtered successively through 125-, 64- and 20-μm Nitex screens. Each size fraction was backwashed onto silver filters which then were frozen. A subsample of each backwash was taken and preserved in 2% Formalin buffered with sodium acetate for taxonomic identification.

Two types of gear were used to collect zooplankton, fish eggs and larval fish. The primary gear was a Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS; Wiebe et al., 1976)

Table 1. Samples collected and analyzed for stable carbon isotope analyses. Numbers under each transect and station refer to cruise dates: 1 = December 1979, 2 = February 1980, 3 = December 1980

Component	Transect and Station					
	A1	A2	A3	B1	B2	B3
Dissolved organic carbon	2	2	2			
Particulates						
>125 μm	3	3	3	3	3	3
20–125 μm	1, 2	1, 2	1, 2	1, 2	1, 2	1, 2
64–125 μm	3	3	3	3	3	3
0.45–20 μm	1, 2	2	2	1, 2	1, 2	2
Zooplankton						
Total	1, 2	1, 2	2	1, 2	1, 2	2
Pooled copepods*	2, 3	2, 3	2, 3	2, 3	2, 3	2, 3
Fish eggs	2, 3	2, 3	2, 3	2, 3	1, 2, 3	2, 3
Larval fish						
Brevoortia	1, 2	1		1, 2	2	
Leiostomus	1	1, 3		2, 3	2	3
Micropogonius	1, 3	1		2		
Mugil		3	3	3	3	3

* Included the copepods *Temora turbinata, Labidocera* spp., and *Oithona* spp. (see text).

consisting of nine 500-μm-mesh nets with a smaller 67-μm-mesh net nested inside each. MOCNESS samples were taken at discrete depths in the upper mixed layer and were pooled with Bongo net (333- and 500-μm) samples taken obliquely from near bottom to surface. Samples were taken every 6 h, pooled according to net size, concentrated by screening, and frozen. Data presented are for composite samples for each 24-h sampling period.

Larval fishes and zooplankton taken from other MOCNESS nets were preserved in 5% Formalin buffered with sodium borate. Larval gulf menhaden (*Brevoortia patronus*), spot (*Leiostomus xanthurus*), Atlantic croaker (*Micropogonias undulatus*), and mullet (*Mugil cephalus*) were later sorted and the gut contents of these larvae identified. Size ranges (length) for the fish analyzed were: 8–23 mm for menhaden; 3–11 mm for spot; 3–12 mm for croaker; and 3–15 mm for mullet. *Oithona, Labidocera,* invertebrate eggs, and pelecypod juveniles were identified in the diet of gulf menhaden, spot, and Atlantic croaker. Three abundant copepod genera, *Oithona, Temora* and *Labidocera,* as well as invertebrate eggs and pelecypod juveniles were sorted from February and December 1980 collections and frozen for isotope analysis; the major component of the material analyzed was the three copepod genera.

Stable carbon ratio analyses (180) were carried out according to Peters et al. (1978). Analyses were made using a Varian MAT 250 isotope ratio mass spectrometer with a precision for replicate carbon analyses of 0.2‰. Results were expressed as parts per thousand (‰) deviations from the PDB standard according to the relation:

$$\delta^{13}C = \frac{^{13}C/^{12}C \text{ of sample} - {}^{13}C/^{12}C \text{ of standard}}{^{13}C/^{12}C \text{ of standard}} \times 1{,}000.$$

Results and Discussion

Our stable carbon isotope data (Table 2) provide strong evidence that carbon fixed by marine phytoplankton, based on analyses of POC >20 μm, is the major carbon source for the planktonic food web in the neritic waters of the northern Gulf of Mexico. Only two components consistently approach terrestrial ^{13}C values: the fine POC fraction (0.45–20 μm) at all stations off the Mississippi River and DOC at the two inshore stations off the River (Fig. 2). The POC fractions >20 μm displayed $\delta^{13}C$ values ranging from a station mean of −21.6‰ (B1) to −23.5‰ (B3) (Table 2), and averaged -22.7 ± 0.16‰ ($\bar{x} \pm$ SE) for both transects; Shultz

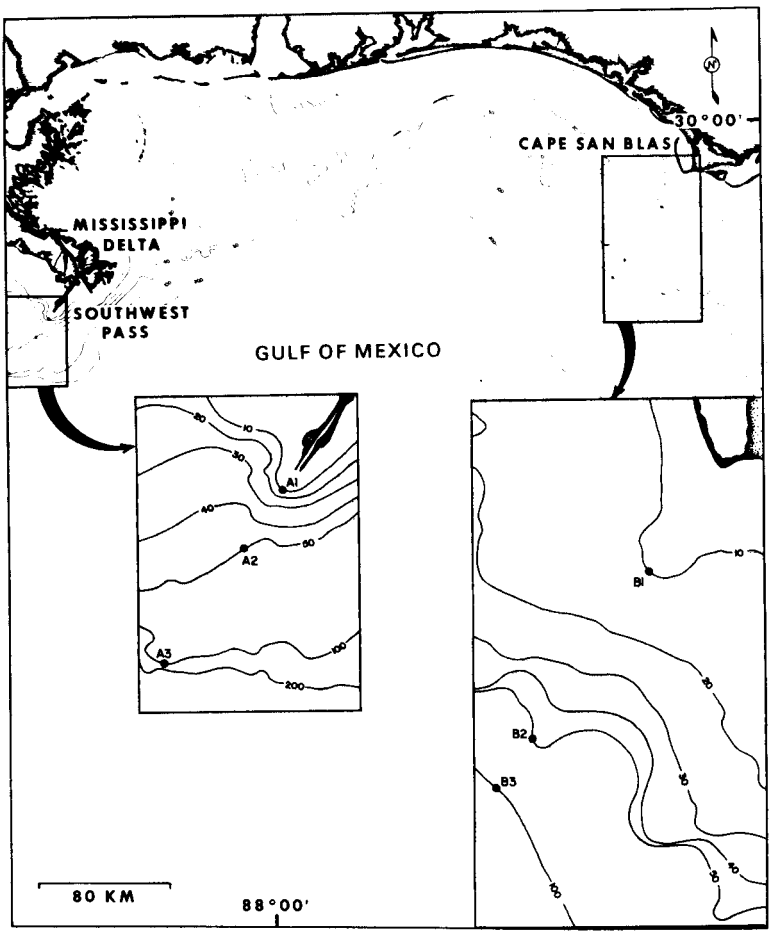

Figure 1. Map of the northern Gulf of Mexico showing location of transects and sampling stations (insets). Isobaths are shown in fathoms.

and Calder (1976) reported a $\delta^{13}C$ value of −26‰ for terrestrial POC in the northern Gulf of Mexico. Our POC values >20 μm are similar to those reported for marine phytoplankton (Smith and Epstein, 1971; Fry, 1977). Microscopic examination of our samples >20 μm from December 1980 revealed that they were dominated by phytoplankton (Table 3); relative dominance of any one species had little apparent influence on the $\delta^{13}C$ value of the sample. DOC displayed $\delta^{13}C$ values ranging from a station mean of −22.2‰ (A3) to −24.3‰ (A2). Values for the two inshore stations (A1, A2) averaged −24‰; Eadie et al. (1978) reported terrestrial DOC values of −26 and −28‰ for terrigenous DOC in the Mississippi River.

Isotope values indicate a dilution of terrigenous carbon with marine carbon for both DOC and fine (0.45–20 μm) POC. We estimated the contribution of terrigenous organic carbon to the isotopic signature of the POC and DOC samples we analyzed with the isotopic mixing equation described by Shultz and Calder (1976). Using the reported terrestrial $\delta^{13}C$ value (−26‰) and the average $\delta^{13}C$ value for

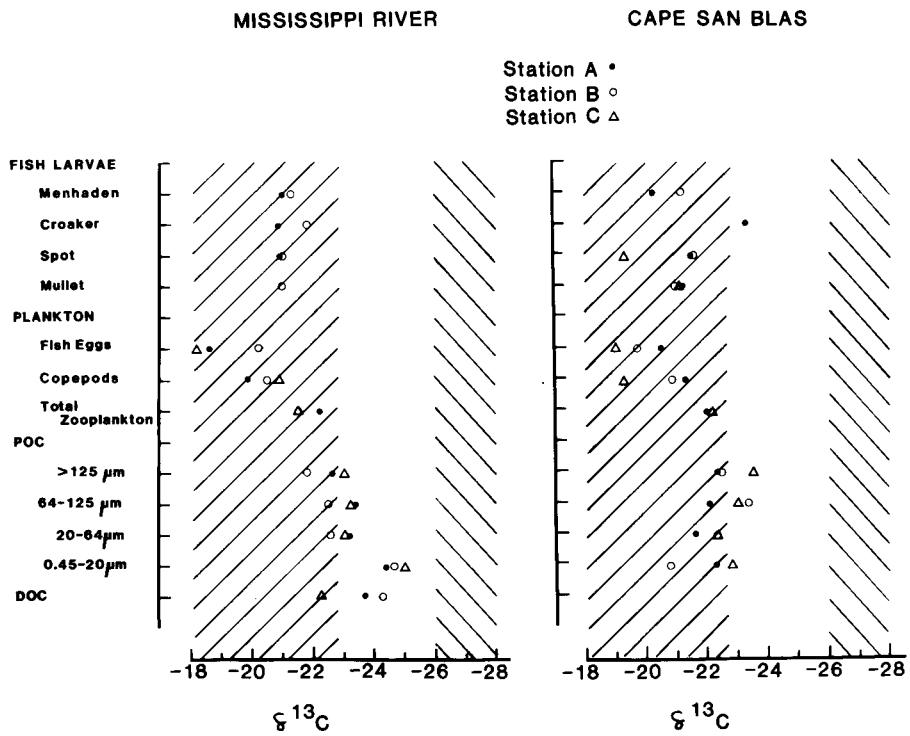

Figure 2. Distribution of station means of $\delta^{13}C$ values for planktonic components analyzed from three stations off Southwest Pass, Louisiana (Transect A) and Cape San Blas, Florida (Transect B). Cross hatched area more positive than −23‰ represents marine carbon; cross hatched area more negative than −26‰ represents terrestrial carbon (see text).

POC >20 μm (−22.7‰) as the marine end-member, we estimated that between 50–70% of the carbon in POC <20 μm along the Southwest Pass transect and about 40% of the carbon in DOC at the two inshore Southwest Pass stations could be derived from terrestrial organic carbon. The isotopic signature of DOC at the offshore Southwest Pass station (A3) appeared to be derived entirely from phytoplankton carbon. It is not surprising to find an association between DOC and the finest POC fraction analyzed, for this particulate fraction may include silt and clay, which can adsorb organic molecules (Greenland, 1971) and which would stay in suspension longer than larger size classes (Postma, 1967; Riley, 1970). In addition, Trefry and Presley (1976) indicated that size classes <64 μm constituted virtually all the suspended sediments off the Mississippi River.

Our data imply that most terrigenous organic carbon discharged by the Mississippi River into the northern Gulf of Mexico settles out of the water column within a short distance (30 km) offshore and does not enter the planktonic food web. Similar observations and conclusions have been made for the Georgia Bight (Haines and Dunstan, 1975; Hanson et al., 1981), where the presence of salinity fronts are possible barriers to outwelled nutrients. Although fronts are not well documented for the Gulf of Mexico, Legeckis (1978) has demonstrated sea surface temperature fronts along the northern Gulf of Mexico coast, and Sackett and Thompson (1963), Parker et al. (1972), Shultz and Calder (1976), and Gearing et

Table 2. Mean values (±SE) of $\delta^{13}C$ for samples collected on three cruises in the Gulf of Mexico (The transect mean ($\bar{x}$) also is presented for each component)

Component	Transect and Station							
	A1	A2	A3	$\bar{x}$	B1	B2	B3	$\bar{x}$
Dissolved organic carbon	−23.7 ± 0.04	−24.3 ± 0.16	−22.2	−23.7 ± 0.34				
Particulates								
>125 μm	−22.6 ± 1.25	−21.8 ± 1.75	−23.0 ± 1.05	−22.5 ± 0.65	−22.3 ± 0.15	−22.5 ± 0.25	−23.5 ± 1.00	−22.8 ± 0.35
64–125 μm	−23.4	−22.5 ± 1.05	−23.2 ± 0.20	−23.0 ± 0.38	−22.1 ± 0.10	−23.4	−23.0 ± 0.05	−22.7 ± 0.27
20–64 μm	−23.2 ± 0.05	−22.6 ± 0.80	−23.0 ± 0.50	−22.9 ± 0.27	−21.6 ± 0.10	−22.4 ± 0.05	−22.4 ± 0.05	−22.1 ± 0.19
0.45–20 μm	−24.4 ± 0.38	−24.7	−25.0 ± 0.0	−24.6 ± 0.23	−22.3 ± 0.45	−20.8 ± 1.76	−22.8 ± 0.13	−21.9 ± 0.61
Planktonic matter								
Total zooplankton	−22.1 ± 0.16	−21.5 ± 0.46	−21.5 ± 0.25	−21.8 ± 0.21	−22.0 ± 0.10	−22.2 ± 0.12	−22.2 ± 0.03	−22.2 ± 0.11
Copepods	−19.9 ± 0.13	−20.5 ± 0.24	−20.9 ± 0.13	−20.4 ± 0.16	−21.3 ± 0.38	−20.9 ± 0.28	−19.3 ± 0.84	−20.6 ± 0.35
Fish eggs	−18.6 ± 1.05	−20.2	−18.2 ± 0.68	−18.6 ± 0.51	−20.5 ± 0.34	−19.7 ± 0.56	−19.0 ± 0.92	−19.9 ± 0.37
Fish species								
Menhaden	−21.0 ± 0.85	−21.3 ± 0.0		−21.2 ± 0.35	−20.3	−21.2 ± 0.55		−20.9 ± 0.45
Croaker	−20.8 ± 0.40	−21.8 ± 0.55		−21.2 ± 0.38	−23.3 ± 0.50			−23.3 ± 0.50
Spot	−20.9	−21.0		−20.9 ± 0.05	−21.5 ± 0.92	−21.6 ± 0.10	−19.3	−21.2 ± 0.61
Mullet		−21.0 ± 0.10	−20.9 ± 0.10	−20.9 ± 0.06	−21.0	−21.2 ± 0.05	−21.0	−21.1 ± 0.07

Table 3. Dominant phytoplankton (percent occurrence) in three particle size categories collected in December 1980 from transects off the Mississippi River (A) and Cape San Blas (B)

Transect and Station:	A1			A2			A3		
Species Size fraction:	>125	125–64	64–20	>125	125–64	64–20	>125	125–64	64–20
Skeletonema costatum	84	75	64	51	19	35	11	25	29
Corethron sp.	—	—	—	—	—	—	—	50	—
Chaetoceros curvisetus	—	13	2	5	19	2	3	11	6
C. decipiens	1	—	—	15	2	—	25	9	10
C. lorenzianus	—	8	1	5	7	2	21	3	9
Thalassionema nitzschioides	2	1	14	—	11	19	3	—	3
Nitzschia sigma	—	—	1	6	11	7	—	—	—
Transect and station:	B1			B2			B3		
Skeletonema costatum	—	—	9	4	3	6	2	5	6
Guinardia flaccida	2	19	1	—	3	—	—	1	—
Rhizosolenia stolterfothii	3	1	26	3	1	11	4	1	13
Bacteriastrum spp.	19	38	3	22	12	2	11	20	5
Chaetoceros diversus	—	8	2	—	5	11	—	3	1
C. lorenzianus	16	6	1	11	5	1	4	1	1
Thalassionema nitzschioides	7	2	8	—	6	5	10	9	6
Thalassiotrix frauenfeldii	2	5	1	10	5	8	19	9	6

al. (1977) all present data supporting the observation of rapid sedimentation of terrestrial organic carbon off the Mississippi Delta. Our samples were taken during winter, the period of maximum water discharge from the Mississippi River (Trefry and Presley, 1976), when abundant detritus should be available for export to the Gulf (Hopkinson et al., 1978). In a recent review of the organic geochemistry of the Gulf, Parker (1981) concluded that particle transport rather than humic substance transport is the major process of movement of terrestrial organic carbon to the shelf, but that only a minor amount, even off large rivers, reaches the Gulf shelf by any process. Outwelled terrigenous organic carbon probably is a major input to the coastal food web of the northern Gulf only within 30 km or less of shore.

Stable isotope ratios of faunal components of the planktonic food web indicate that phytoplankton, rather than terrestrial POC, is the ultimate carbon source and that some fractionation (Degens et al., 1968a; b) of stable carbon isotopes occurs between trophic levels. Total zooplankton $\delta^{13}C$ values ranged from a station mean of −21.5, to −22.1‰ off Southwest Pass and from −22.0 to −22.2‰ off Cape San Blas (Fig. 2), values that are within the range reported for marine phytoplankton at lower latitudes (Haines, 1976; Fry et al., 1977; Fry and Parker, 1979; Haines and Montague, 1979). The difference between isotopic ratios of phytoplankton (−22.7‰) and of our total zooplankton (mean = −21.9‰) is about 0.8‰ while the difference is 2.2‰ between phytoplankton and copepods. These differences are estimates of trophic level fractionation and are similar to reported values of 0.8 ± 1.1‰ (DeNiro and Epstein, 1978) and an assumed value of 1.5‰ (McConnaughey and McRoy, 1979). Had total zooplankton and copepod components derived their carbon from the fine POC fraction (0.45–20 μm), trophic level fractionations would be 2.8‰ and 4.2‰, respectively, at the two inshore Southwest Pass stations. If terrigenous carbon (−26‰) alone were the primary carbon source, trophic fractionation values would exceed 4‰ for both zooplankton components. These disparities are generally beyond reported trophic level isotopic

fractionation values, and thus we conclude that terrestrial carbon is not trophically transferred to zooplankton.

The mean $\delta^{13}C$ of fish eggs (mixed species) was more positive than values we obtained for larval fishes (Table 2) and more negative than the mean value of adult fish (−17.5‰, range −14.8 to −19.2‰) collected in the offshore Gulf of Mexico by Fry and Parker (1979). The disparity among the $\delta^{13}C$ values for fish eggs, larval fish and adult fish may reflect a differential isotopic ratio of high protein and lipid reserves in the eggs or dietary differences between the adult females that spawned the eggs and that of the resulting larvae. The diet of an organism normally is reflected in the $\delta^{13}C$ value of its tissues and also may be reflected in the $\delta^{13}C$ of developing eggs. Fry and Parker (1979) compared $\delta^{13}C$ values of lipid-extracted and non-extracted muscle from adult red and vermillion snapper collected from the Gulf. They indicate that differing amounts of lipid were not responsible for the $\delta^{13}C$ difference observed between the two species, and suggest that the disparity probably results from dietary and metabolic differences. Fish larvae have a diet different from that of their adults and could be expected to exhibit a different $\delta^{13}C$ value.

The uniformity of the larval fish isotopic ratio data indicates that zooplankton probably serve as the intermediate transfer link between phytoplankton and larval fishes in the northern Gulf of Mexico. Mean larval fish isotope ratio values were similar to each other and to the planktonic components analyzed (Table 2). Of the 39 analyses performed for larval fishes, only two $\delta^{13}C$ values were more negative than −23‰: spot (−23.8‰) from Cape San Blas (B1) in February 1979 and croaker (−24.4‰) from the same station in December 1980. Although these values may indicate some utilization of terrestrial carbon, the overall larval $\delta^{13}C$ mean (±1 SE) for the four species for both transects (−21.1 ± 0.19‰) was intermediate to mean values for total zooplankton (−21.9 ± 0.11‰) and copepods (−20.5 ± 0.30‰).

Gut analyses support the conclusion derived from stable carbon isotope ratios that zooplankton constitute the major transfer pathway of phytoplankton carbon to larvae of spot, croaker, and white mullet, but not to larvae of gulf menhaden, which appear to derive their carbon directly from phytoplankton as well as through the intermediate zooplankton link. There was diet overlap between menhaden (643 analyzed), spot (135), and croaker (173), but phytoplankton occurred consistently and only in menhaden. A microplanktonic dinoflagellate (*Prorocentrum* spp.), tintinnids, and juvenile copepods were found in menhaden; juvenile and small adult copepods, invertebrate eggs, tintinnids, pteropods and juvenile pelecypods were the major diet of spot; and juvenile and adult copepods were most prevalent in croaker. White mullet appeared to feed primarily on copepods; of 114 analyzed, 84 had copepod parts in their gut. Thus, based on abundance of food items in the gut, larval menhaden are more directly linked to phytoplankton than are the other three species. An isotopic fractionation of about 1.8‰ was calculated for the phytoplankton-larval menhaden trophic transfer step, a value within the expected range (DeNiro and Epstein, 1978); in reality, the trophic fractionation value probably lies between 1‰ and 1.8‰ because of the mixed phytoplankton and zooplankton diet.

Our data indicate that in the northern Gulf of Mexico the carbon of the highest trophic level examined, larval fishes, is derived from marine phytoplankton either directly or through zooplankton, not from terrigenous carbon sources. Most terrigenous POC apparently settles out within about 26 km from the mouth of Southwest Pass. Our observations coincide with $\delta^{13}C$ values for sediments off the same area (Gearing et al., 1977). Extant terrestrial carbon off Southwest Pass

appears associated with DOC (40% terrestrial carbon) and the finest POC fraction (0.45–20 μm) analyzed (50–70% terrestrial carbon). The carbon transfer pathway, based on isotopic ratio analyses of zooplankton and larval fishes and on gut contents of larval fishes, appears to be primarily from phytoplankton to zooplankton and then to larval spot, croaker, and white mullet. Gulf menhaden larvae appear to derive their carbon directly from phytoplankton as well as through an intermediate zooplankton link. Isotopic fractionation occurred at each transfer step. Most trophic level differences did not exceed ±1.8‰, a range similar to that reported for both laboratory and field studies.

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